division, or when environmental conditions change? When and how are magnetosomes attached? Does this relate to magnetite crystallization and orientation? How does the position and polarity of the magnetosome chain relate to other important cellular structures, such as flagella? And finally, how did this structure evolve? Magnetotactic bacteria are somewhat scattered in phylogenetic terms, but how likely is it that magnetosomes evolved independently more than once? Indeed, genes for magnetosome synthesis and organization are clustered on the *M. gryphiswaldense* genome and contain numerous insertion elements that facilitate recombination, so lateral transfer of this gene set between species may be fairly easy [20]. More genetic and genomic analysis will be needed to address this issue.

We'll close this foray into magnetotaxis with one last twist. Simmons *et al.* [6] recently reported substantial populations of south-seeking magnetotactic bacteria co-existing with north-seeking bacteria at a site in the northern hemisphere (Falmouth, Massachusetts, USA), not far from where Blakemore's samples first revealed magnetotaxis. The north and south-seeking bacteria were significantly stratified, with the south-seekers most abundant in more highly oxidized locations. The south-seekers Simmons *et al.* [6] observed are morphologically distinct from known magnetotactic species, but have not yet been isolated and cultured for laboratory investigation. How and why these bacteria have adapted magnetotaxis to generate a distinct behavioral response is as yet unknown. Future investigations should yield more insight into mechanisms by which microbes coordinate magnetotaxis with other sensory systems to find their way home — and perhaps provide clues as to how macroscopic creatures generate and utilize cellular-scale magnetic structures for their own ends.

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# Social Evolution: Cooperation by Conflict

**A recent study suggests that aggression between wasps depends upon the costs and benefits of fighting, as determined by the position of individuals in a dominance hierarchy.**

**Tabitha M. Innocent and Stuart A. West**

In a world where individuals are destined to be selfish, conflict seems likely. As described by Darwin's 'survival of the fittest', all individuals are motivated by the need to survive and reproduce, passing their genes on to future generations. Each individual acts upon their own best interests, but what is best for one individual will not necessarily be ideal for another. Thus individuals can prefer different outcomes, and inevitably, this often leads to a conflict of interests. Conflict ranges from the peacefully resolved competition amongst male lion coalitions, for access to oestrus females [1], to the aggressive and often lethal fighting observed between wingless male fig wasps [2].

Whilst conflict is inevitable, aggression is less easily explained. In general, animals avoid fighting — and thus avoid serious injury — through ritualistic assessment of opponents [3]. In most species this 'conflict

Figure 1. Each individual *P. dominulus* wasp is marked with a unique colour combination, allowing the activity of all individuals to be followed. (Photograph by M. Cant.)

limitation' is the evolutionarily stable strategy [3], giving the highest fitness returns. Thus the critical question faced by an individual is not why to fight, but when to fight. The answer depends upon the ratio of costs incurred through aggression, to benefits accrued as a result of aggression, in terms of the fitness of that individual. Many factors influence the costs and benefits of aggression, including the number and density of competitors, the value of a contested resource, the relatedness between competitors, and an individual's relative fighting ability [4,5]. The current value of a resource depends upon future resource opportunities: male lions do not fight over particular females, as many future reproductive opportunities exist [1]. In contrast, wingless male fig wasps emerge and mate within the fig fruit, and so their reproductive success is limited to the females emerging in the same fruit. Consequently, when there are few females, the males are prepared to risk death during violent conflict [6].

A recent study by Cant *et al.* [7] takes things in an exciting new direction by investigating how a dominance hierarchy (social structure) can influence the costs and benefits of aggression. They produced a model of conflict between individuals of adjacent social rank, generating predictions that they then tested in the paper wasp *Polistes dominulus*. Their model assumed a group of related females, with a dominance hierarchy where the top individual breeds, and the other individuals help them. When dominance hierarchies are composed of relatives it complicates the evolution of conflict [8]. Cant *et al.* [7] predicted that the rate of aggression should vary with: position in the dominance hierarchy; value of the resource to be inherited (colony productivity); and time left to acquire the resource. Why should these factors matter? The reason is that the presence of a dominance hierarchy directly influences the individual cost:benefit ratios of engaging in conflict. Whilst cost varies little with rank, the fitness benefits of winning increase exponentially with the probability of inheriting the dominant position in the group, towards the front of the inheritance queue. Thus the benefits of aggression increase with increasing rank, and therefore greater aggression should be seen between higher-ranking individuals.

*P. dominulus* is an excellent organism for testing these predictions (Figure 1) [7]. In the Spanish population studied, nests are founded by groups of 1–10 usually related females, who form a dominance hierarchy with the top-ranking female laying most of the eggs, and the lower-ranking subordinates providing most of the help. As predicted, aggression rates were found to decrease with decreasing rank, in accordance with potential fitness returns. With an elegant manipulation, it was also shown that rank 2 individuals promoted to rank 1 dramatically increased aggression rates. This clearly demonstrates that aggression level is proportional to cost:benefit, rather than individual quality. Although colony productivity had no influence, the overall rate of aggression increased through the founding period. This is because, as the season progresses towards its end, the chance of peacefully obtaining dominance through the death of higher-ranked individuals decreases. Consequently, it becomes relatively more beneficial to risk life and limb in a battle for control of the group.

Given that the dominance hierarchy is so influential, how does it arise? In this study system, the dominance hierarchy is unrelated to either individual quality or the relatedness between individuals. Cant *et al.* [7] suggest that it may be determined by some convention such as order-of-arrival or age. A possibly interesting consequence of the hierarchy is that it could lead to lower-ranked wasps helping at a higher rate, because this is how they will maximise their inclusive fitness. This suggestion has wider implications for the study of social species, raising the possibility that, if a dominance rank can be formed, it could provide a mechanism for reducing conflict between individuals, and hence favour higher levels of cooperation [9]. This could provide an analogous case to the removal of worker laid eggs by other workers, in the social insects. This 'worker policing' maximises inclusive fitness of individuals, but has the additional benefit of selecting against worker reproduction and hence reducing conflict within colonies [10]. Do dominance ranks provide a solution to the problem that the same factors that keep individuals together to potentially cooperate, can also keep them together to compete [11]? It is both interesting and ironic that by looking at aggression, insight is found into the enigma of cooperation.

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# Vertebrate Segmentation: Snail Counts the Time until Morphogenesis

**During segmentation of vertebrate embryos, unsegmented mesenchymal mesoderm is divided into epithelial segments called somites. This process is governed by oscillating gene expression of the somite clock. A recent paper identifies the transcription factor *Snail* as a link between the somite clock and the control of somite morphogenesis.**

**Scott A. Holley**

Somitogenesis is the process by which the segmented precursors to the vertebral column and musculature are generated during vertebrate embryogenesis. Morphological segmentation occurs when cells within the anterior of the mesenchymal presomitic mesoderm epithelialize to form bilateral pairs of somites (Figure 1). This process is reiterated in an anterior to posterior direction, adding new somites as the embryo grows at its posterior. Morphological segmentation is governed by the somite clock, which creates oscillations in gene expression — predominantly of genes in the Notch pathway — within the mesenchymal presomitic mesoderm. These oscillations manifest themselves as repeated cycles of activation and repression of transcription, thus creating stripes of gene expression that traverse the presomitic mesoderm in a posterior to anterior direction (Figure 2) [1]. In the anterior presomitic mesoderm, these stripes of mRNA expression represent the positional information that determines the location of each somite boundary [2]. While numerous studies have elucidated aspects of the molecular control of somite morphogenesis and the genetic basis of the somite clock, a recent paper by Dale *et al.* [3], identifies Snail proteins as the most direct link between the clock and control of somite morphogenesis.

Snail proteins are zinc-finger containing transcriptional regulators that appear to control various aspects of cell morphology and cell migration. Specifically, Snail proteins promote mesenchymal morphology at the expense of epithelial morphology by down-regulating the expression of components of adherens junctions, such as *E-cadherin* and desmosomal proteins such as *desmoplakin* [4]. During chick and mouse embryogenesis, *Snail* expression is initiated as cells undergo an epithelial to mesenchymal transition while entering the primitive streak [5,6]. Dale *et al.*, [3] show that *Snail* expression oscillates in the presomitic mesoderm and disappears in the anterior presomitic mesoderm as cells undergo a mesenchymal to epithelial transition as each somite forms. Thus, *Snail* expression correlates spatially and temporally with the mesenchymal morphology of the somite precursors. Accordingly, they find that ectopic expression of *Snail* in the chick embryo prevents epithelialization of somite precursors in a cell-autonomous manner. Together these observations suggest that *Snail* regulates somite morphogenesis [3]. Unfortunately,

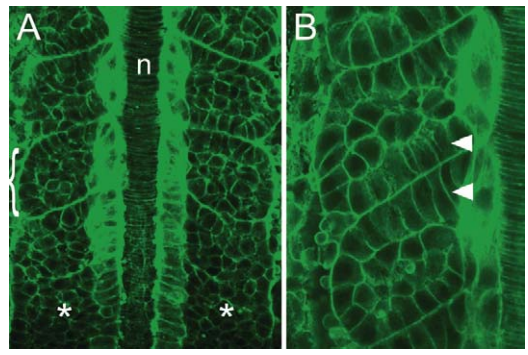


Figure 1. Somite morphogenesis as exemplified in zebrafish.

(A) Somites form in bilateral pairs from the mesenchymal presomitic mesoderm (asterisks). The most recently formed somite is indicated by the bracket, and 'n' indicates the notochord. (B) Somites are epithelial spheres surrounding a mesenchymal core of cells. The columnar epithelial cells are indicated by the arrowheads. Shown are confocal images of phalloidin-Alexa488 stainings of zebrafish somites (courtesy of Dörthe Jülich). In both panels, anterior is up.